ECOLOGICAL COLOR VARIATION
IN A BUTTERFLY
AND
THE PROBLEM OF "PROTECTIVE COLORATION"
WILLIAM HOVANITZ

THE DISTRIBUTION AREA OF *Oeneis chryxus* Dbld. & Hew. (Lepidoptera: Satyridae) extends from the arctic regions of North America, south through the high ranges of the Rocky Mountains, the Sierra Nevada and the Great Basin as far south as New Mexico. The butterfly is not uniformly distributed over this area but is found only in the Arctic-alpine life-zone and in the unforested ridges of the upper Hudsonian; hence, in the southern parts of its range, it is restricted to isolated "islands" on the higher peaks. The species is variable with respect to the predominant color on the upper surfaces of the wings, some individuals being a rather dark yellow-brown, others a medium yellow-brown and in extreme instances, yellow-white. The colors appear to be entirely quantitative in nature; individuals showing all different intermediate shades of color can be arranged from darkest to lightest. Within a restricted population, however, the individuals are remarkably uniform and only very occasionally are atypical examples found. Most populations consist of individuals of a rather dark yellow-brown color; occasional ones consist of extremely light or extremely dark forms.

In California and western Nevada, the species is represented by two races, a very pale, yellow-white race (*ivallda* Mead, fig. 5B) and a very dark, yellow-brown race (*stanislaus* Hov., fig. 5D). The distribution area of each of these races is shown on the map (fig. 1); the localities where the white race has been found are shown by circles and those of the brown race by triangles. The contour line shown on the map approximately encloses the habitable territory of the species, this being the Arctic-alpine and upper Hudsonian life-zones. The color shade of individuals inhabiting the various localities is shown on the
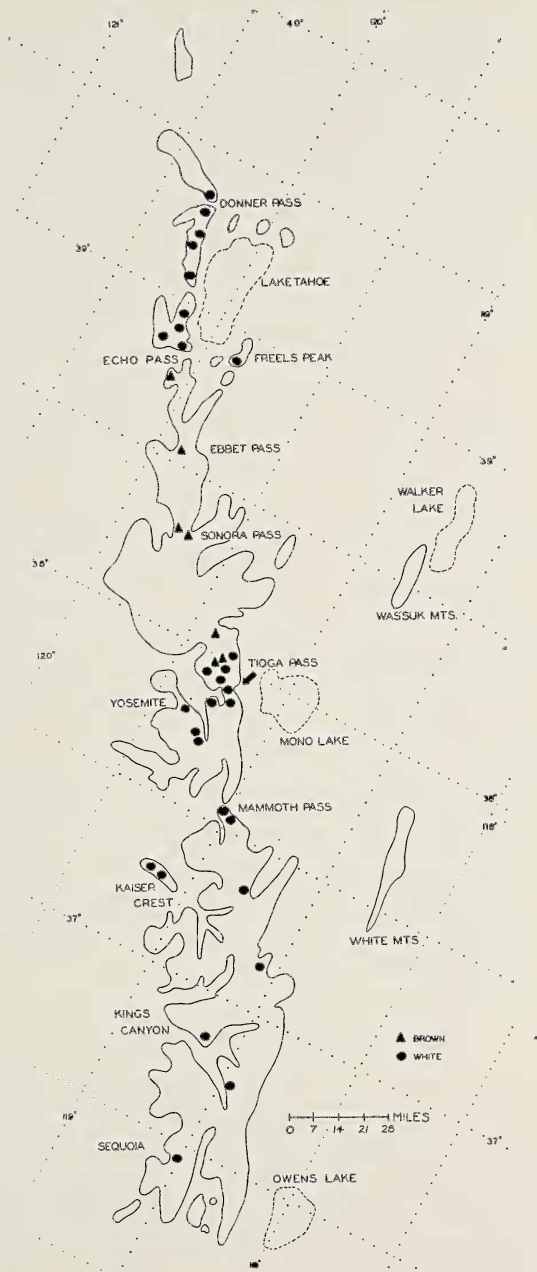
Fig. 1.—Map showing extent of Arctic-alpine and upper Hudsonian life-zones in the Sierra Nevada of California and the mountains of western Nevada. Localities where *O. chryxus ivallda* has been recorded are designated by a circle and those of *O. chryxus stanislaus* by a triangle.

diagram (fig. 2). The horizontal scale indicates the geographical position of the locality while the vertical scale indicates the shade of color, darkest at the top and lightest at the bottom; the line connecting the points gives an index of the steepness of the variation gradient (*cline* as used by Huxley, '39) between the localities. At Sonora Pass, in the center of the range of the brown race, white or light-colored individuals are taken very rarely. Between Ebett and Echo Passes the populations all lighter in color, but entirely white individuals are as yet unknown. South of Sonora Pass to a point north of Tioga Pass where the brown and white races appear to interbreed, the population of the brown race is nevertheless dark, showing no variation gradient. In the very narrow transition zone, however, the population is mixed, showing the entire range of variation from the darkest to the lightest. These facts would seem to indicate that the differences between the brown and white races are not due to a single gene, but rather to a combination of several genetic factors, and that these factors or genes are widely distributed throughout the entire range of the species though with differential concentrations. As far as one can judge without genetical experimentation, the white races from the northern and southern sections are entirely identical even though the intervening area inhabited by the dark race is at least eighty miles in extent. The shortest means of communication between the two regions is through that occupied by the brown one (fig. 1). Furthermore, as the surrounding territory is of lower elevation and is in a different life-zone, it is ecologically unsuited for the existence of this particular species; it could hardly be a region through which migration could take place. That is the status of the variation, but what is the origin of the color races and what are the reasons for their present distribution?

ORIGIN OF THE COLOR RACES

A discussion of the origin of the color races can only be speculative and theoretical, but the evidence available does allow one to comment upon several alternatives. It may be postulated: (1) That the Sierra Nevada was once entirely populated by a white race and that the brown race has either originated *de novo* in the central part or that it has come in via the high Basin Ranges from other populations of the brown form; (2) That the Sierra Nevada was once populated entirely by a brown race at
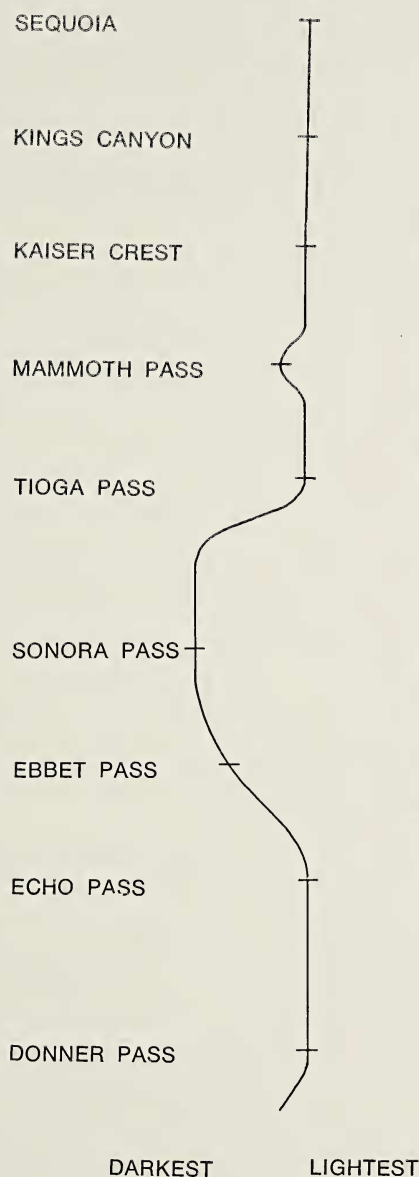
Fig. 2.—Diagram showing the shade of yellow-brown coloration typical for populations of *Oeneis chryxus* at various localities in the Sierra Nevada. The data from which this is derived were not photometrically studied (because of the lack of facilities) nor compared with a set of color standards (because the correct shade and tints were unobtainable); comparsions were made with arbitrary standards of the material itself. The diagram is, therefore, not to be taken too exactly.

either end of which genes for whiteness developed greater concentrations, or (3) That a uniform population never did exist in the Sierra Nevada. A discussion concerning these could not be conclusive when there is a total lack of paleontological evidence, but some pertinent information can be given. For example,

A. No other populations of white individuals exist in any part of the range of *Oeneis chryxus* and yet the two identical white races exist isolated from each other at the present time in the Sierra Nevada.

B. The light and dark races are interfertile and interbreed on the borders of their ranges, at which places intermediate individuals are produced. Continued interbreeding over a period of years should tend to eliminate the differences between them and produce a uniform, intermediate-colored population.

C. No other white races exist which would tend, by migratory individuals, to increase the concentration of white-producing genes in the northern and southern Sierra Nevada. Other brown races do exist which could increase the concentration of brown-producing genes. Individuals from these populations (in the Rocky Mountains) could more easily reach the Sierra Nevada via the high Basin Ranges which form a series of "stepping-stones" across the uninhabitable desert areas of that region than via any other way. These are most numerous in the region directly east of the central Sierra Nevada at Sonora Pass. Other things being equal, were the influx of brown-producing genes sufficient to produce this central, brown race in the first place, it should be sufficient to change the entire Sierra Nevada populations into a single brown race.

One is forced, therefore, to ask the following questions: If the brown-producing genes have gained in concentration without the external help of migrations, what factors have allowed this increase over white-producing genes or vice versa, if the white-producing genes have gained in concentration without the external help of migrations (and it is definitely impossible to do otherwise in this case), what factors have allowed this increase over the brown-producing genes? Also, if the brown-producing genes have gained in concentration *with* the aid of migrations, what factors have prevented further spread into the regions now with greatest concentration of white-producing genes? If a uniform population never existed in the Sierra Nevada, what factors have prevented such a uniformity from becoming established and what has been the causal agent of the specific distributions observed?

REASONS FOR THE OBSERVED DISTRIBUTION

As a result of the evidence above, it can only be assumed that selection of some sort has been operative in producing the observed distributions of the white and brown races. The problem is to find the differential factors allowing for selection and then to find the specific mechanism of selection. All the possible factors which have been thought to have any bearing on selection may be placed under one of these three groups: differences in the climate, the food or the habitat. The first, climate, is not likely to be such a factor because within the Sierra Nevada, the white and the brown races inhabit the same life-zone and the white race lives both north and south of the brown race (humidity decreases southward). It may be assumed that there is no difference in general climate affecting the selection of one race in preference to the other, except wherein this may be due to some other factor indirectly. The second group, food, is likewise probably not a factor because as far as the information is available at present, the food plants of the larvae of both races are the same, namely, species of alpine grasses; more data on this subject, of course, is needed. Only in the third group, habitat, can we find a striking difference in the environment of the two races; this is in the color of the ground rock, which is the most obvious feature of the landscape above timberline (figs. 3 and 4). Soil cover at the elevations where *Oeneis chryxus* lives is scarce, and the alpine meadows where there is any considerable amount are unsuitable as a habitat. The insect lives almost exclusively on rocky terrain and the rocks, rather than plants or soil, give the predominant color to the landscape. The rock in the northern and southern Sierra Nevada, where the white race is found, is predominantly a white granite (fig. 5A). On the contrary, in the distribution area of the brown race, the central region, the mountain tops are composed of dark red rocks (fig. 5C). Jenkins ('38) and personal observations show that the country above timberline from Echo Pass to a point south of Sonora Pass is composed mostly of dark-red Tertiary volcanics and of red Miocene andesite. North of Echo Pass, as well as in a greater part of the range above timberline from north of Tioga south to Sequoia, a very light-colored Jurassic granite is decidely predominant. The accompanying photographs (figs. 3 and 4) illustrate the characteristic difference in the coloring of the

Fig. 3.—High Sierra Nevada in the Yosemite-Tioga Pass region showing the granitic aspect of the country at timberline where the white race occurs.
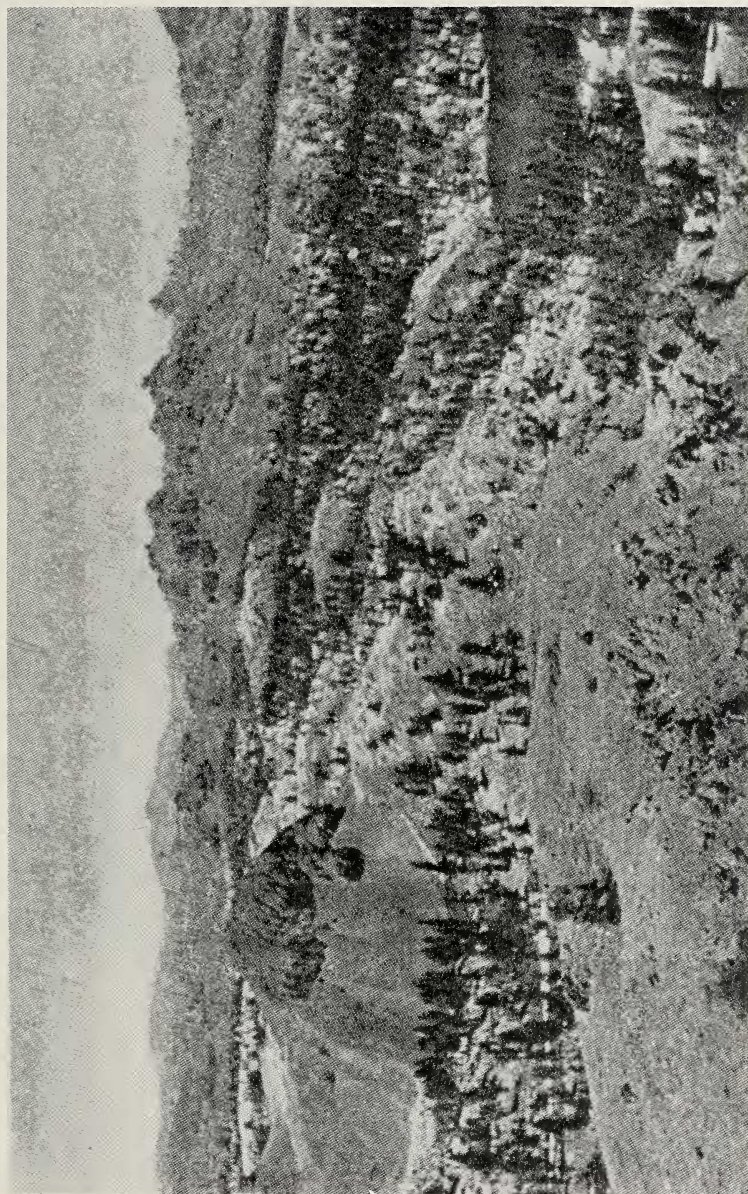
Fig. 4.—High Sierra Nevada in the Ebbet Pass region showing the dark, volcanic aspect of the country at timberline where the brown race occurs.
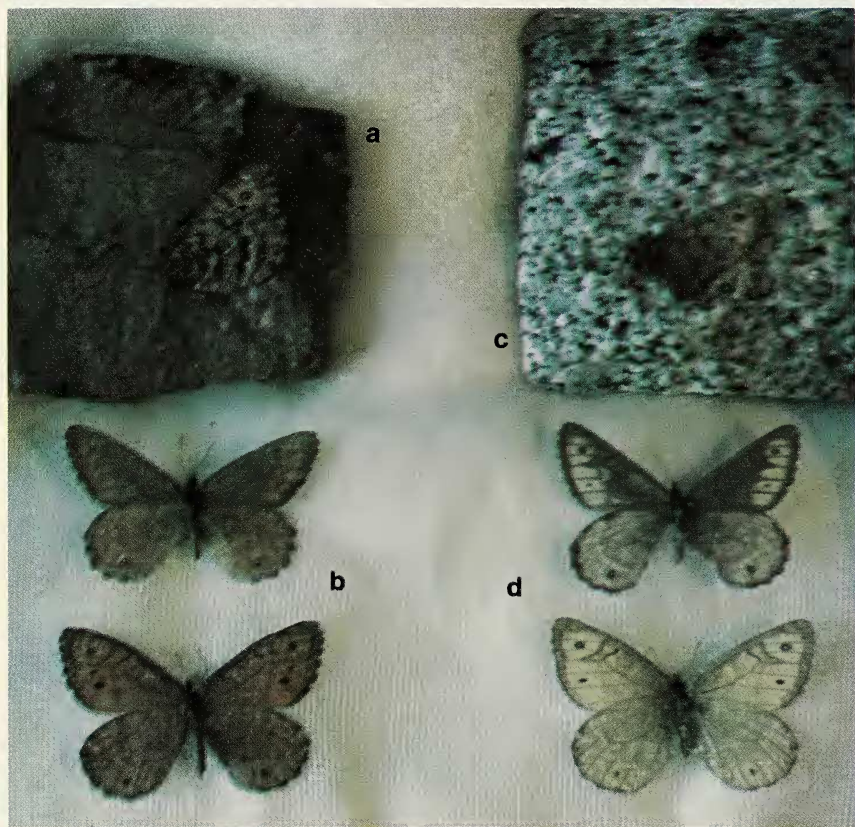
Fig. 5.—(A) An andesite rock and a specimen of the dark race with
wings closed. (B) Upper surfaces of *Oeneis chryxus stanislaus* show-
ing the predominantly darker color. Top specimen is a male and the bottom
one is a female. (C) A granitic rock and a specimen of the white race
with the wings closed. (D) Upper surfaces of *Oeneis chyxus ivallda* show-
ing the predominantly white color. Top specimen is a male and the bottom
one is a female.

landscape. The distribution map (fig. 1) shows that the ranges of the brown and white races almost exactly coincide with the distribution of the different kinds of rock. The presence of the more gradual gradient (fig. 2) at the northern part of the brown races' distribution can be explained by the fact that in this region there is a decreasing percentage of dark rock in relation to the light as one proceeds northward. To the south, the change is more abrupt. The "humps" seen in the diagram are also explained on the same basis; areas of dark rock are of increasing abundance in these regions.

Since the relation between the color of the butterfly and the color of the rock is the only relationship observed, the cause or mechanism of the selective effect must be found. Two possibilities are open, namely, selection by predators or selection by physiological fitness for the environment. If selection by predators is involved, one must first be able to find the predators and second, one must be able to discover that the protective color is really an aid in concealment from these predators. These requirements are seldom fulfilled in the very voluminous literature dealing with real or supposed protective coloration or mimicry. Even some most recent writers have not done this (e.g. Dice and Blossom '37; Benson '33) but appear merely to have assumed that the correlation between the coloration of some races of mammals and that of the ground on which they live is due to protection from predators. The actual proof of selection by predators (or by any other means) on any living thing in nature has not yet been shown; in fact, in most cases of supposed protection by protective resemblance, it has never been shown that the actual effective natural predator is selective on account of the supposed protection. Shull ('37) states that it is not up to the opponents of the mimicry theory to disprove the statements of the proponents, but rather the latter must present experimental evidence in favor of it first. Dobzhansky ('37; p. 164) states: "Taken as a whole, an unprejudiced observer must, I think, conclude that an experimental foundation for the theory of protective resemblance is practically non-existent." The experiments of di Cesnola ('04), Beljajeff ('27), Sumner ('35), Carrick ('36), Isely ('38), Reighard ('08) and others were conducted to prove or disprove whether cryptic or warning coloration is a factor of differential selection of prey by predators. Some of these have proven that cryptic coloration gives a selective advantage to the posessor of this coloration under the artificial conditions of

predator pressure prevailing when and where the experiments were carried out, and at most can only be suggestive of wider implications. Whether or not the prey is under such predator pressure in nature and whether or not such "protective" coloration is effective or necessary under these conditions is another thing to be proven; certainly the prey must be allowed to protect itself by its own specific habits and mode of living. Heikertinger ('33-'36) and McAtee ('32) have criticized the mimicry theory rather thoroughly but neither's evidence is sufficient or convincing enough to be effective. Pearl ('30) states as the basic and minimal requisites of an observational or experimental demonstration that natural selection has altered a race in any particular instance the following: "A. Proof of somatic difference between survivors and eliminated. B. Proof of genetic differences between survivors and eliminated. C. Proof of effective time of elimination. D. Proof of somatic alteration of race. E. Proof of genetic alteration of race." No author has yet satisfied these, nor has anyone shown why one species rather than another is better adapted for existence on account of the protective colors which it possesses. Ironically enough, it would appear that the animals getting along best in nature are those which are not "protected." This should not be considered as evidence against natural selection but only as a reminder that some things can be carried too far; modern genetics assumes natural selection to be true since a method by which a genetic population change could come about any other way is unknown. In regard to *Oeneis chryxus*, it can only be stated that an unbiased student must look into all factors of the environment and this has seldom been done by any observer of "protective coloration."

A search for predators of the adult *Oeneis chryxus* has not been successful. There is no known difference (that is, no visible difference observed) between the two races in the immature stages (larvae and pupae) and they are therefore irrelevant in this connection. The adults fly only during the warmer part of the day when there is sunlight; other times they are at hiding in the relative darkness which exists between rocks, among alpine plants and such places where color is of no value. Predators, therefore, in order to be selective, must prey upon the butterflies during that very limited time of day, and chiefly when they are in flight,[1] for only at that time is the color difference shown to its greatest advantage. Other insects and birds seem to be the only predators under these conditions. Grinnell and Storer ('24) list

only *Leucosticte tephrocotis dawsoni* Grin. (the Sierra Nevada
Rosy Finch) and *Zonotrichia leucophrys leucophrys* (Forster)
(Hudsonian white-crowned Sparrow) as whole or part time
residents in the Arctic-alpine life-zone. These birds are seed
eaters but occasionally capture insects. Observations have not
shown them to eat *Oeneis* but these observations can only be
classed as negative evidence, and not conclusive. No observations
have shown other insects to eat *Oeneis* either, though further
study will definitely be needed.

As stated above, there appear to be no general climatic dif-
ferences between the various parts of the Arctic-alpine life-zone
in the Sierra Nevada to which physiological differences between
the color races of *Oeneis* might be attributed. However, micro-
geographic differences could exist, these being caused by differ-
ent edaphic conditions, such as warmer microtemperature near
the food plant due to a greater absorption of solar radiation by
the dark-colored rocks. Developing larvae and pupae might be
affected by the absorption of different wave-lengths of solar
light (color), or by the absorption by the larvae of different
chemical constituents from the food plant, which likewise might
have been chemically different on account of the absorption
from soil of different composition. These are factors which have
received little attention from experimenters possibly because of
the predatory-selection idea and cannot be verified at the present
time. But as the color differences are almost certainly genetic,
it cannot be assumed that the above effects change the color
of the butterfly directly.[2] It may be that if a given mutated gene
or, more probably, a new combination of genes (which gives
the brown or white color as a bi-product) gives the insect which
possesses it greater suitability for living in the habitats where
the above conditions prevail, it might have a greater chance for
survival.

---

[1] *One of Carrick's ('36) conclusions was that movement renders as
void any protective resemblance present. However, the results of this paper
should not be taken too seriously; there is great doubt as to the statistical
significance of the experiments made. Movement has been mentioned by
many naturalists as the basic factor rendering a concealed object conspicu-
ous; its truth is much less difficult for a critical mind to imagine than some
cases of "resemblances."*

[2] *The color differences are assumed to be most probably genetic be-
cause white populations exist and develop upon dark-rock areas where
these areas are smaller than the effective breeding range of an individual
butterfly. White individauls from the granitic region surrounding such an
isolated dark-rock area could easily swamp and make ineffective any selec-
tive effect which might be operative.*

Perhaps it may be stated that eco-genotypical variation as illustrated by the species *Oeneis chryxus* is of more common occurrence among animals than is generally acknowledged. Since most of the published data of this sort have been among the vertebrate animals, the dogma of natural selection by predation (true though it may be in many instances) has overwhelmed any theory of ecological fitness. An account of the parallel between the genetic variation and ecological preferences is being prepared which may lead to an experimental verification of the parallel between the physiological conditions of the habitat and the genetics of color in animals.

ACKNOWLEDGMENTS

SUMMARY

The distribution of the color races of *Oeneis chryxus* in the Sierra Nevada is described. It is found that the races differ mainly in the color of the upper surfaces of the wings and that this coloration is found to be very closely correlated with the color of the habitats in which these races live. The question is raised as to the reason for this correlation and hypotheses are advanced and discussed to account for this "protective coloration," namely, selection by predators and selection by physiological fitness for the environment. The latter is thought by the author to be too severely neglected in cases of this sort and possibly to be the most probable hypothesis in this instance.

APPENDIX

Localities from Which the Material was Collected

Collections made in June, July or August or sporadically since 1907. ("S" means "several.")[3]

COUNTY	LOCALITY	ELEVATION	NUMBER
Nevada	Castle Peak Ridge	8,500	about 15
"	Donner Summit	8,000	unknown
"	"Truckee"	—	—
Placer	Deer Park	7,900	1
"	Snow Mt.	—	1
"	Ward Peak	8,800	S
"	Ellis Peak	—	4
"	Ellis Peak	—	S
El Dorado	Mt. Tallac	9,000	30±
" "	Fallen Leaf Lake	—	S
" "	Pyramid Peak	10,000	—
" "	Echo Lake	8,000	S
—	"Lake Tahoe"	—	many
Amador	Silver Lake	8,000	3
Alpine	Freel's Peak	—	S
"	Ebbet Pass	9,500	11
"	Sonora Pass	8,500	13
"	Sonora Pass	10,000	2
"	Sonora Pass	10,000	125+
"	Sonora Pass	10,000	28
Tuolumne	Slide Canyon	10,500	1
"	Slide Canyon	10,500	1
"	North Peak, Conness	—	10±
"	Young Lakes	—	4
"	Gaylor Lakes	11,000	15
"	Tioga Pass R. Sta.	10,000	3*
"	Tioga Lake	10,000	6
"	Tioga Peaks	11,000	34
"	Mt. Dana	11,000	4
"	Mt. Gibbs	10,000	1
"	Mt. Dana	—	—
"	Mammoth Peak	10,000	S

[3] *Most of this material was personally checked by the author; a small part of it was not and error could have come in in this part. However, all the more important localities were either collected in or the material was checked by the author.*

APPENDIX—*Continued*

COUNTY	LOCALITY	ELEVATION	NUMBER
Mariposa	Cathedral Lake	10,000?	—
"	Florence Lake	11,000?	—
"	Mt. Lyell	12,000?	—
Mono	Virginia Lakes	—	S
"	Minaret Summit	9,000	9
"	Mammoth Pass	9,000	1
"	Mammoth Crest	10,000?	2
"	"Mammoth"	—	many
"	Red Mt.	11,000?	4
"	Red Mt.	11,000?	10
"	Red Mt.	11,000?	10
"	Panorama Dome	—	4
"	Red Lake	—	2
"	Barney Lake	—	1
"	Duck Summit	—	—
"	Duck Lake	—	16
"	Skeleton Lake	—	1
"	Rock Creek	11,000	1
Fresno	Huntington Lake	—	1
"	Huntington Lake	—	—
"	Kaiser Crest	10,000	140
"	Mt. Hutching's Ridge	10,450	1
"	Bubbs Creek	10,500	1
Inyo	Bishop Creek	—	—
Tulare	Mineral King	—	1

LITERATURE CITED [4]

BELJAJEFF, M. M. 1927. Ein Experiment über die Bedeutung der Schutzfärbung. *Biol. Zentralbl.* 47: 107-113.

BENSON, S. B. 1933. Concealing coloration among some desert rodents of the southwestern United States. *Univ. Calif. Pub. Zool.* 40: 1-70.

CARRICK, R. 1936. Experiments to test the efficiency of protective adaptations in insects. *Trans. Roy. Ent. Soc. Lond.* 85: 131-140.

DI CESNOLA, A. P. 1904. Preliminary note on the protective value of colour in *Mantis religulosa. Biometrica* 3: 58-59.

DICE, L. R., and P. M. BLOSSOM. 1937. Studies of mammalian ecology in southwestern United States with special attention to the colors of desert mammals. *Carnegie Inst. Wash. Pub.* 485.

[4] *References here are not to be considered to constitute a bibliography in any sense; further references may be found in those cited.*

DOBZHANSKY, TH. 1937. Genetics and the origin of species. *Columbia Univ. Press.*

HEIKERTINGER, F. 1933-36. Kritik der Schmetterlingsmimikry, I-V. *Biol. Zentralbl.* 53: 561-590, 54: 365-389, 55: 461-483, 56: 151-166, 463-494.

HUXLEY, J. S. 1939. Clines: An auxiliary method in taxonomy. *Bijdragen Tot De Dierkunde* 27: 491-520.

ISELY, F. B. 1938. Survival value of acridian protective coloration. *Ecology* 19: 370-389.

JENKINS, O. P. 1938. Geologic map of California. *Dept. Nat. Resources, State of California.*

McATEE, W. L. 1932. Effectiveness in nature of the so-called protective adaptations in the animal kingdom, chiefly as illustrated by the food habits of the Nearctic birds. *Smithsonian Misc. Coll.* 85: No. 7, 1-201.

PEARL, RAYMOND. 1930. Requirements of a proof that natural selection has altered a race. *Scientia* 7: 175-186.

REIGHARD, J. 1908. An experimental field-study of warning coloration in coral-reef fishes. *Carnegie Inst. Wash. Pub.* 103: 257-325.

SHULL, A. F. 1937. The needs of the mimicry theory. *Science* 85: 496-498.

SUMNER, F. B. 1935. Evidence for the protective value of changeable coloration in fishes. *Amer. Nat.* 69: 245-266.